Plant Signaling & Behavior 5:6, 763-765; June 2010; © 2010 Landes Bioscience

When do arbuscular mycorrhizal fungi protect plant roots from pathogens?

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Key words: arbuscular mycorrhizal fungi, *Fusarium oxysporum*, root architecture, pathogen protection, multi-functionality

Submitted: 03/10/10

Accepted: 03/10/10

Previously published online: www.landesbioscience.com/journals/psb/article/11776

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Addendum to: Sikes BA, Powell JR, Rillig MC. Deciphering the relative contributions of multiple functions within plant-microbe symbioses. Ecology 2010; 91:1591–7.
and
Sikes BA, Cottenie K, Klironomos JN. Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. J Ecol 2009; 97:1274–80.

Arbuscular mycorrhizal (AM) fungi are mainly thought to facilitate phosphorus uptake in plants, but they can also perform several other functions that are equally beneficial. Our recent study sheds light on the factors determining one such function, enhanced plant protection from root pathogens. Root infection by the fungal pathogen *Fusarium oxysporum* was determined by both plant susceptibility and the ability of an AM fungal partner to suppress the pathogen. The non-susceptible plant species (*Allium cepa*) had limited *F. oxysporum* infection even without AM fungi. In contrast, the susceptible plant species (*Setaria glauca*) was heavily infected and only AM fungi in the family Glomeraceae limited pathogen abundance. Plant susceptibility to pathogens was likely determined by contrasting root architectures between plants, with the simple rooted plant (*A. cepa*) presenting fewer sites for infection. AM fungal colonization, however, was not limited in the same way in part because plants with fewer, simple roots are more mycorrhizal dependent. Protection only by *Glomus* species also indicates that whatever the mechanism(s) of this function, it responds to AM fungal families differently. While poor at pathogen protection, AM fungal species in the family Gigasporaceae most benefited the growth of the simple rooted plant species. Our research indicates that plant trait differences, such as root architecture can determine how important each mycorrhizal function is to plant growth but the ability to provide these functions differs among AM fungi.

Arbuscular mycorrhizas (AM) represent the oldest and most widespread symbiosis with land plants.[1] Most mycorrhizal research has focused on the ability of AM fungi to facilitate nutrient uptake, particularly phosphorus.[2] Although researchers recognize that AM fungi are multi-functional,[3] it is not clear what factors determine which function an AM fungus performs or its relative importance to the plant.[4] Newsham et al. (1995)[3] hypothesized that AM function is based on root architecture: plants with simple rooting systems are dependent on mycorrhizas for nutrient uptake, while those with complex root systems are less dependent on mycorrhizas for nutrient uptake, but are more susceptible to root pathogens because of increased numbers of infections sites.[3] These two functions, phosphorus uptake and enhanced pathogen protection from mycorrhizas also depend on the identity of the fungus. Arbuscular mycorrhizal fungi in the family Gigasporaceae are more effective at enhancing plant phosphorus, while AM fungi in the Glomeraceae better protect plants from root pathogens.[5]

Our results support both plant and fungal control of a common pathogen, *Fusarium oxysporum*, and the interaction between these two factors ultimately determined the level of pathogen infection and plant mycorrhizal benefit. We inoculated two plant species that have contrasting root architectures with one of six AM fungal species from two families (or no AM fungi). After five months of growth, plants were inoculated with *F. oxysporum*, grown for another month and then harvested. All plant seeds and fungi were collected in a local old field community.[6]

Allium cepa (garden onion) was not susceptible to *F. oxysporum* likely because it has only a few adventitious roots below the main bulb that do not present many sites for infection. In contrast, *Setaria glauca* (yellow foxtail) was heavily infected by *F. oxysporum* and has fine roots with increased numbers of branching points and lateral meristems where fungi can colonize.[7] For the susceptible plant (*S. glauca*), AM fungal species from the family Glomeraceae were effective at reducing pathogen abundance while species from the Gigasporaceae were not. Forming a symbiosis with a *Glomus* species resulted in *S. glauca* plants that were as large as control plants. AM fungal species from the family Gigaspoaceae were more beneficial to growth of the simple rooted *A. cepa*, which had fewer roots to take up soil nutrients.

Reduced rooting structures may limit pathogen infection sites, but AM fungal colonization was not limited in the same way and may actually alter plant root architecture. While the simple rooted *A. cepa* had limited pathogen susceptibility, it had twice the AM fungal colonization of the complex rooted *S. glauca.* Because the simple rooted plant has a greater dependence on mycorrhizas,[8] it likely transmits chemical signals to rapidly initiate mycorrhizal formation,[9] but then may have less control on the spread of AM fungi within the root. In contrast, *S. glauca* is more susceptible to fungal pathogens and may be less mycorrhizal dependent in nature.[10] As a result, *S. glauca* may treat all colonizing root fungi as potential parasites. Colonization by AM fungi from the Glomeraceae was also much greater than those in the Gigasporaceae due to differences in fungal life history strategy between these families.[11,12] AM fungal colonization can reduce root branching in plants and alter plant allocation to roots, thereby increasing mycorrhizal dependence for nutrients[10,13] and potentially reducing pathogen infection sites. Mycorrhizal induced changes to plant root architecture may therefore reinforce current mycorrhizal associations and alter future fungal colonization attempts.[14] An important next step is to test if AM fungal families (or species) alter plant root architecture in different ways and the degree to which these effects depend on colonization timing and the plant host.

Our study did not isolate the particular mechanism by which AM fungi control pathogens, but this mechanism clearly differentiates between AM fungal families. AM fungi can control pathogens through several mechanisms including direct competition for colonization sites, indirect initiation of plant defensive responses or altering other rhizosphere biota.[15] Although these AM fungal families differ in the intensity of root colonization,[11] percentage of root length colonized by an AM fungus is a poor predictor of pathogen limitation compared to family identity,[12,16] suggesting that direct competition for space is unlikely. AM fungi share many cell surface molecules with pathogenic fungi like *Fusarium*.[17] These molecules can act as signals that initiate plant production of defensive compounds such as phytoalexins, phenolics and other compounds.[18] While AM fungi appear to evade these defenses, only AM fungal species in the family Glomeraceae would have elicited plant responses which altered future infection by *F. oxysporum*. AM fungi in the Gigasporaceae may differ more from *F. oxysporum* in their chemical signals or not colonize roots sufficiently to induce a sustained, system-wide plant response. In addition, many rhizosphere related microbes are antagonistic to pathogenic fungi[15] and may differ in their response to the different AM fungal families.[19] Because rhizosphere microbes also differ among plant species, plant pathogen protection may be influenced by multiple ecological interactions that determine the specific cases when mycorrhizal pathogen protection occurs. To distinguish between these mechanisms, future experiments could test whether biochemical similarity or ecological similarity (especially with other soil biota) between an AM fungus and fungal pathogen can predict mycorrhizal induced pathogen protection.

Plant and fungal identity clearly affect AM fungal function and benefit, but to accurately use AM fungi in agriculture and restoration[20,21] we must clearly understand how functional mechanisms differ. Different mycorrhizal functions may be based on common plant traits like root architecture, but ecology, colonization timing and environment may alter the specific function AM fungi provide and its importance to plants. While it may be useful to establish greenhouse rules about which fungal species perform specific mycorrhizal functions, predicting their role in more complex systems relies on understanding if other factors will enhance or negate these effects. Most AM fungal species vary in their ability to perform each function and these can be locally adapted to limiting soil nutrients.[22] In plants, there is also a range to which specific mycorrhizal functions may benefit plant fitness, and these responses are based on both plant traits (which change throughout a plant's life cycle) and the local environment.[23,24] Given this variation, it is critical to understand if AM fungi can respond to cues from the plant or the environment to identify what factors limit plant growth and whether a the most effective AM fungus shows a greater response.

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